

TRIBAL REVISIONS IN THE ASTERACEAE. VIII.

A NEW TRIBE, URSINIEAE

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The nearly forty to more than fifty species of Ursinia form a very natural genus found throughout South Africa and extending into East Africa. Of the many tribes common in the same area, Ursinia resembles the Anthemideae in habit and the Arctotideae in superficial features of the flowering head. The genus has been placed in both of these tribes and has been considered intermediate between them. A complete reevaluation of the relationship of Ursinia has been possible through the use of microscopic observation. The limits of the two tribes, Anthemideae and Arctotideae, have been greatly clarified in the process.

The genus Ursinia was first described by Joseph Gaertner in 1791 citing Arctotis flosculus radiantibus sterilibus, paleis coloratis disco longioribus, foliis bipinnatis linearibus Linn. Syst. Veg. 792 which equals Arctotis paradoxa L. as a synonym, but Gaertner described another closely related species. Gaertner made comparisons with other valid species of Arctotis which have superficially similar phyllaries and pappus. Cassini (1816), putting emphasis on style branches, placed the genus in his Anthémidées. Lessing (1832) followed by DeCandolle (1836) altered the tribal concepts and changed the placement of Ursinia. They recognized the differences in style branches between Arctotis and Ursinia, but the prominent pappus and the large enveloping paleae of Ursinia caused them to place the genus in the Senecionidae subtribe Helenieae among the Madieae. The latter is a well marked and very different group almost exclusively in Western North America with two genera in the Hawaiian Islands and one species in Chile.

Bentham (1873) restored a tribal concept more like that of Cassini, but he deemphasized style branch differences in placing Ursinia in the Arctotideae. Bentham's comments were, "The genus Ursinia (including Sphenogyne) forms a distinct group of about 54 species, all S. African, although one of them reappears in (or extends into) Abyssinia, differing from Arctotideae generally in their truncate style-branches, their paleaceous receptacle, and glabrous foliage. It appears to me, however, to be more nearly connected with Euarctoteae than with any other tribe or subtribe. De Candolle placed it among Helenieae, where it has certainly no connexions, structural or geographical. The peculiar paleae of the pappus, distinctly convolute-contorted in

their arrangement, are much more those of Arctotis itself than of any Helenioideae. The habit and involucre connect them with some Anthemideae of the northern type, as well as with several of the true S. African Euarctoteae". The Bentham treatment was followed by Hoffmann (1894).

The concept of Ursinia as intermediate between the Anthemideae and Arctotideae has been retained by most general treatments and the view was summarized in part by Cronquist (1955) who made a number of instructive comments. "A number of species of Arctotis (sens. lat.) have scarious-tipped and -margined bracts, recalling the Anthemideae, and if Bentham is to be followed in placing Ursinia in the Arctotideae near Arctotis, no consistent differences are left between the Arctotideae as a whole and the Anthemideae. Hoffmann, while pointing out the anthemideous habit and style of Ursinia, retained the genus in the Arctotideae, partly because of its well developed pappus. Even if Ursinia is transferred to the Anthemideae (where it would still be anomalous and without apparent close relatives), the fact that so keen a student as Bentham was led to put it in the Arctotideae bears witness to the relationship between the two tribes".

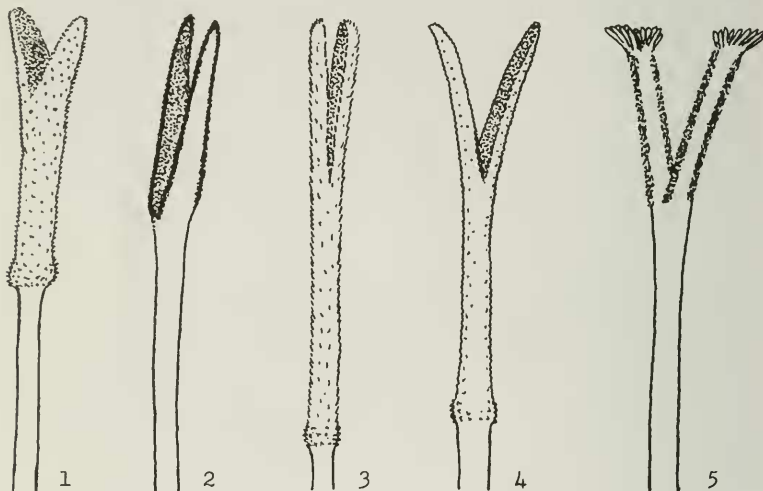
By the time of Cronquist's study there was already some rather definite evidence giving more support to Cassini's original disposition of Ursinia. Beauverd (1915) in a study involving nervature of the ray flowers, structure of the hair on phyllaries and flowers, and corolla glands concluded, ". . . les Ursinia ne sauraient être maintenus dans la tribu des Arctotidées" ". . . Le Genre Ursinia constitue une section particulière de la tribu des Anthémidées". This disposition was followed by Merxmüller in two 1954 publications and by Prassler (1967) in her monograph of Ursinia. Prassler classified Ursinia "zu de Anthemideae, wo die Gattung allerdings wegen ihres gut ausgebildeten Pappus eine ziemlich isolierte Stellung einnimmt".

Recent literature has provided considerable information on the cytology of the tribes under consideration here. The chromosome numbers of the genus Ursinia are summarized by Haesler (1967) with twelve citations of  $n = 8$  and one citation of  $n = 7$ . Three additional counts by Nordenstam (1967) are all  $n = 8$ . Nordenstam mentions the counts known for the various genera placed in the Anthemideae,  $x = 6, 7, 8, 9, 10, 13$  and  $17$ . The numbers of the Arctotideae seem to be  $x = 9$  for Arctotis (Darlington & Wylie 1956),  $x = 5$  for two genera of the Gorteriinae (Nordenstam, 1967), and  $x = 7$  for Berkheya (Darlington & Wylie, 1956).

The results of the present study are in three parts, (1) delimitation and relationship of the tribe Arctotideae, (2) delimitation of the tribe Anthemideae, and (3) the description of the tribe Ursinieae.

## ARCTOTIDEAE

The most marked features of the tribe Arctotideae are the presence of distinct ray and disk flowers, the produced and partially caudate bases of the anthers, and the rather short-branched scabrous styles. The styles are particularly distinct in the stigamic area which covers the complete inside surface of the branches and the dense scabrosity which covers the entire outer and lateral surface to a point well below the origin of the branches. The scabrosity ends rather abruptly in a usually swollen more papillose ring well down the shaft of the style.



Figures 1-5. Styles of Arctotideae and Ursinieae. 1-2. Arctotis stoechadifolia Berg., 1. Disk flower. 2. Ray flower. 3. Hirpicium bechuanense (S.Moore) Roessler. 4. Berkheya carduoides (Less.) Hutch. 5. Ursinia anthemoides (L.) Poir.

Such a style is unique to the Arctotideae and various members of the Cynareae. For the most part the styles of the ray and disk flowers are much alike but in Arctotis the styles of the rays may become quite differentiated.

Additional features of the Arctotideae observed in this study include details of the stamens, corolla and pappus. The anther appendages are usually broadly oblong or triangular, longer than wide, and essentially flat. A few examples may be slightly concave abaxially. The exothelial cells vary from forms with thickenings primarily on the lateral walls as in Arctotis to forms with evenly slightly thickened walls as in most of the Gorterinae. In Berkheya, Cullumia and Didelta there are

irregular thickenings and lacunae with thickenings more prominent at the ends of the cells. The pollen is also notable for the two basic types. The pollen of Arctotis and its segregate genera or subgenera is simply spinose as is the pollen of the more distantly related genus Didelta. In contrast, the pollen of the Gorteriae as seen in Gorteria, Gazania, Hirpicium, Berkheyopsis, Cullumia and Berkheya has a reticulating surface pattern with or without distinct spines at the junctures of the reticulations. The concept of the tribe devised here would exclude Platycarpha which has distinctive pollen with internally complex exine.

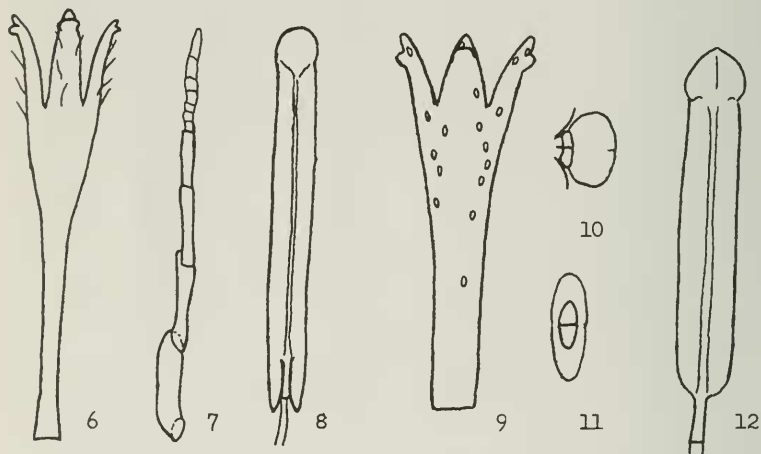
Corolla characters are subtle but significant. All genera of the Arctotideae have glands that are rather long-stalked with small tips. The apical cells are thinner walled than the basal cells. Such glands are generally like those of the many members of the related tribe Cynareae but are very unlike those of Ursinia and the Anthemideae. Disk corolla lobes of the Arctotideae are elongate as in the Cynareae, Vernonieae, Liabeae and Mutisieae. These lobes are strikingly different from those of Ursinia and the Anthemideae. The lobes of the Arctotideae have stomates along the lateral margins and near the veins in all but one genus, Cullumia. In the latter genus the lateral margins are almost completely encased in slender sclerotized cells and stomates have not been seen. Even here stomates might show in stained material. The stomates are like those seen in many species of Liabum in the Liabeae. Such stomates are not present in Ursinia or the Anthemideae and they have not been seen in any of the Cynareae that have been examined.

Conclusions regarding the limits of the tribe Arctotideae are as follows. The genus Heterolepis which Cassini placed in the Arctotideae but which Bentham removed to the Inuleae, has a style precisely like the Arctotideae and it should be returned to that tribe. The genus has a setose pappus consisting of rather broad short-fringed setae. The pollen is spinose and not reticulate. The genus seems closest to Didelta which has a short but setose pappus. Perhaps more significant, the two genera are alike in possessing vestigial anthers in the ray flowers.

Platycarpha has pollen with a prominent complex columnar structure in the thickened rather smooth exine. Such pollen has been seen in most of the genera of the Cynareae that have been sampled but not in any of the Arctotideae. The margins of the corolla lobes are also like the Cynareae in the lack of stomates. The corolla glands have distinctly larger apical cells than any of the Arctotideae. The genus is evidently better placed in the Cynareae.

Ursinia has a truncated style branch that is mostly smooth abaxially with a separate stigmatic line along each lateral margin of each branch. The genus is also different in the broad deeply concave anther appendages and unproduced bases of the thecae, in the corolla lobe shape and structure, and in the form

of the corolla glands. More obvious differences in Ursinia are the paleaceous receptacles and the habit. Even the cellular detail of the pappus squamae is very different from the plain-walled abaxially scabrous squamae of Arctotis with which they have been compared. The only really favorable comparisons are in the scarious tips of the phyllaries, the abaxial outgrowth near the tips of most corolla lobes, and the tendency for lateral thickenings on the elongated exothecial cells, these characters not being unique to these groups. It is evident that Ursinia must be excluded from the Arctotideae and that it and the Anthemideae are not even closely related to the Arctotideae.



Figures 6-12. Flower parts of Arctotis and Ursinia. 6-8. Arctotis angustifolia L. 6. Corolla. 7. Gland from corolla. 8. Stamen. 9-12. Ursinia caledonica (Phill.) Prassler. 9. Corolla. 10-11. Lateral and end views of glands from corolla. 12. Stamen.

It is notable that the Arctotideae seem to have a series of characters that are shared by a whole succession of tribes such as the Vernonieae, Liabeae, Cynareae, Mutisieae and Cichorieae. These have styles with a single stigmatic area covering the inside surface of the branches, anthers with bases projecting well below the point of attachment, appendages essentially flat, and lobes of the disk flowers long and narrow. The combination of characters in the monotypic African genus Eremothamnus helps further to tie the various tribes in this series together. Among these tribes are all the members of the family having reticulate patterns on the surface of the pollen.

In contrast, Ursinia and the Anthemideae seem to belong to a totally different group having styles with two distinct stigmatic lines on the branches. The lines throughout the group seem to be separated by at least a median groove even when shifted onto the inner surface of the style branch. In this series are all those forms with the thecae of the anthers not extending noticeably below the point of attachment to the filament. In this series are found all the Asteraceae with short lobes on the disk flowers, with keeled anther appendages, or with sterile unbranched styles.

There are still many characters that might either extend or alter this concept. For example, some Vernonieae have glands on the anther appendages, a character known otherwise from only the Heliantheae, Helenieae and Inuleae.

#### ANTHEMIDEAE

The most widely recognized features of the tribe are the usually dissected leaves, the short paleaceous or absent pappus, the noncaudate anthers, and the truncate style branches. Many of the members also have distinctive odors. In areas where synantherologists have been most active such as Europe and North America, the tribe has been very accurately circumscribed. Nevertheless, the present study has found genera from a number of other areas that have been misplaced in the tribe. The new delimitation is on the basis of a number of characters in addition to those previously noted in the literature.

As recognized here the Anthemideae have four rather constant characters, the style, the exothecial cells, the glands of the corolla, and the pollen.

The tip of the style is always truncate with a marginal brush of hairs or papillae. Such a style is found again in many Senecioneae and Inuleae but not in any other tribes. In other tribes where the style branches are blunt the details of the structure are different.

The exothecial cells of the Anthemideae have thickenings primarily on the lateral walls. Such exothecial cells are also characteristic of the Astereae and they occur in many Senecioneae and Inuleae, in part of the genus Tridax in the Heliantheae, in some of the Arctotideae and perhaps elsewhere. Such cells do not occur in any Helenieae or in other members of the Heliantheae that have been examined.

The Anthemideae have corollas with short lobes bearing no stomates. The outer surface of the corolla in every genus examined has at least some glands and these are mostly of a distinctive form. The typical gland has a stalk that is very short and usually sunken into the corolla surface, and the cap cells are extremely enlarged. Even more distinctive is the

extent to which the glands are laterally compressed with the cells of each of the two rows as high as wide. The basal attachment of the glands forms a distinctive vertically elongate oval or somewhat diamond-shaped section bisected by a transverse wall. Glands of this precise type have been noted thus far only in the Anthemideae and in Ursinia.

The pollen of the Anthemideae is spherical and tricolpate with or without spines. The grains are consistently distinct from those of all closely related tribes (Astereae, Inuleae, Heliantheae, Senecioneae) by the slightly thickened exine with columnar structure internally that is visible under the high power lens of the compound microscope. Such internal structure is found also in many Cynareae and Mutisieae, but in these there is more variation and the grains are generally different in size and shape. The pollen character might be regarded more lightly in the Anthemideae if every genus that had different pollen didn't have other significant differences too. Genera that have been placed in the Anthemideae that would be excluded on the basis of pollen include the following.

Isoetopsis Turcz. of Australia, in addition to the pollen difference has style branches that are not truncate and glands on the corolla that are small-headed and not laterally compressed. The genus also has large squamose pappus setae unlike the members of the Anthemideae. The genus has anthers that are perfectly representative of members of the tribe Astereae. No other characters being in conflict, the genus Isoetopsis is regarded here as a member of the Astereae.

Plagiocheilus Arn. ex DC. of South America, in addition to the pollen difference has styles that are not truncate and small-headed glands without lateral compression. The ray achenes are in many rows and are strongly compressed. The exothecial cells of the anthers have thickenings often on the transverse walls and the apical appendages are reduced but the genus is evidently a member of the Astereae rather close to Lagenophora and Solenogyne.

Abrotanella Cass. of Southern South America, New Zealand and New Guinea, in addition to the pollen difference has anthers that are often short-caudate at the base and corollas that are without glands or hairs. The exothecial cells have thickenings on the transverse walls. The genus falls easily into the tribe Senecioneae. There are even prominent laticifers running up the middle of the corolla lobes as is common in the Senecioneae.

Ischnea F.v.Müll. of New Guinea, in addition to the pollen difference has corollas without glands or hairs, and exothecial cells with thickenings on the transverse walls. Mattfeld (1929) suggested the genus was related to Abrotanella. Mattfeld was correct to the extent that both genera are members of the Senecioneae, but Ischnea is more closely related to Crocidium of Western North America.

The previous four genera are all forms having achenes of the disk flowers usually sterile and the disk styles non-

functional. These are all that have been seen of the genera with sterile disk achenes in the Hoffman concept of the Anthemideae. Further study may prove that all genera with such disk flowers should be excluded from the Anthemideae.

Ursinia Gaertn. of Africa, in addition to the pollen difference has a well developed pappus of large expanded squamae with distinctive cellular structure and anther appendages that are broader and more concave. Of the various genera lacking the pollen type of the Anthemideae, Ursinia is the only one showing any real relationship, having habit, corolla lobes and corolla glands of the same type. Style branches are like those of the Anthemideae in all respects. There remains the choice of treating the genus as a member of the Anthemideae differing by two very basic characters, or treating it as a separate but related tribe. We chose to follow the precedent of others who have excluded the genus from the Anthemideae. In this way both tribes become readily definable in their major characters. It makes little sense to destroy a workable tribal concept by including an anomalous genus that is without immediate relatives in the tribe.

#### URSINIEAE

Tribus nova Asteracearum. Plantae herbaceae vel frutescentes erectae vel procumbentes paucae vel multo ramosae. Folia alterna integra vel lobata vel bipinnata. Capitula in scapis elongatis axillaribus singularia; squamae involucri multiseriatae interiores ad apicem late scariosae; receptacula manifeste paleacea; corollae albae, flavae, cupreae vel purpureae glanduliferae, glandulis subsessilibus grosse capitatis lateraliter compressis; radii sine antheris; corollae discoideorum 5-lobatae, lobis extus valde procurrentibus; thecae antherarum inferne ecaudatae, cellulis exothecialibus elongatis plerumque ad apices et pro parte minore lateraliter noduliferis, appendicibus late obovatis abaxialiter valde concavis non glanduliferis; styli florum discoideorum in nectariis non vel parum immersi, ramis ad apices truncatis annulate fimbriatis, linis stigmaticis binis lateralibus; pappus magnus 1-2-seriatus raro nullus, squamis 5 exterioribus laevibus interdum costatis, squamis interioribus 5 vel rarius deficiens setaceis plerumque haud aequilongis interdum brevissimis. Grana pollinis sphaerica ca. 25  $\mu$  diam regulariter spinulifera, exineibus interne ut videtur simplicibus.

The tribe contains the single genus, Ursinia. Prassler (1967) in her monograph of the genus, recognized 37 species using broad concepts. The type was given as Ursinia paradoxa Gaertn. = U. chrysanthemoides (Less.) Harv. Two subgenera were recognized; subgenus Ursinia with the pappus in 2 rows; and subgenus Sphenogyne with the pappus in 1 row or in 1 species lacking.



The various distinctive features of the Ursinieae include the anther appendages, the pollen and the pappus. The appendages are very broadly ovate, as wide as long or wider, and very deeply concave abaxially. Appendages of the Anthemideae are sometimes rather broad and concave but never to the same extent.

The pollen of Ursinia is clearly distinct from that found in all confirmed members of the Anthemideae, but it is the basic type seen in other related tribes such as the Astereae. It is likely that the Ursinia pollen reflects a more ancestral type and that the pollen of the Anthemideae is a derived type.

The pappus is the most prominent of the distinct features of Ursinia. The most comparable type previously placed in the Anthemideae was that consisting of about 8 large overlapping squamae in Isoetopsis. The transfer of the latter genus to the Astereae eliminates this only example.

The cellular structure of the pappus of Ursinia is one of its most distinctive features. The individual cell ends do not project as in most squamose types of pappus, the surfaces are completely smooth. In addition, the walls show prominent spiral thickenings around their entire cell surfaces instead of the more common type of ornamentation restricted to the intercellular surfaces. The spiral thickenings of Ursinia may vary greatly in pitch from cell to cell and the older cells show a tendency to unravel as thin parts of the wall give way. In the most highly differentiated pappus types such as in U. annua Less. the squamae also show a very prominent costa of more layers of thicker-walled cells.

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